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The Hexandrous Species of *Topobea* (Melastomataceae)

by

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A key and updated geographic and taxonomic notes are presented for the five known species comprising the hexandrous clade of *Topobea*. *Topobea arboricola*, a Panamanian endemic described and illustrated here, is distinguished by its six stamens per flower, 2-locular ovary, elliptic to ovate leaves with a caudate-acuminate to long-attenuate apex, and unappendaged anther connectives.The need for recording field data on taxonomically useful floral and fruit characters is emphasized.

RESUMEN

Se describe una especie nueva, *Topobea arboricola* de Panamá. Se proveen descripciones, notas sobre distribución y fenología, y discusiones referentes a las afinidades de las cinco especies de *Topobea* que tienen seis estambres. También se presenta una clave y mapas de la distribución para todas ellas. El color y tamaño de los pétalos y estambres, forma de los poros de las anteras, y el número de lóculos en el ovario son a menudo caracteres taxonómicos muy útiles en *Topobea*.

Topobea, with approximately 70 species, is a berry-fruited genus of mostly shrubby epiphytes and hemiepiphytes restricted to wet forests of tropical America. Over 55 species occur in the biodiversity hotspot extending from Costa Rica south to Colombia.

Traditionally, *Topobea* has been defined by its 6-merous isomerous flowers with 12 stamens, 6-locular ovary, and elongate anther thecae with broad confluent apical pores. Although this characterization applies to a majority of species in *Topobea*, discovery of new species in southern Central America in the past two decades has necessitated a broadened circumscription of the genus to accommodate the accumulation of new and unusual species and a reconsideration of generic limits between *Topobea* and its sister genus *Blakea* (Almeda 1990).

I here provide a review of the most specialized evolutionary line within the genus that I informally refer to as the hexandrous species. These species, which are largely centered in Panama, share several synapomorphic characters that include: (1) 6-merous flowers with six stamens, each of which is attached to the hypanthial torus opposite a calyx lobe; (2) subsessile or short-pedunculate flowers; and (3) 2-locular or 4-locular completely inferior ovaries. Until recently, most of the species treated here were known from few collections. A study of additional material generated by my recent field work and that of colleagues now makes it possible to emend and augment morphological and distributional information for described species, propose another new species in this alliance, and provide a preliminary assessment of interspecific relationships within this well-defined clade.

Understanding intraspecific variation in woody epiphytes has always been a challenge. Many epiphytic species of Melastomataceae are composed of widely dispersed, low density populations. This coupled with spotty sampling by collectors and the fragmentary preservation or loss of critical

floral characters on dried specimens has contributed to the paucity of adequate study material. Petal shape and color, stamen number, morphology of anther pores, and ovary locule number are essential characters for the delimitation of species in *Topobea*. Unfortunately, some of these characters are difficult to evaluate once specimens have been pressed and dried. Ideally, notes on these characters should be recorded in the field, if the preservation of flowers and fruits in a liquid medium is not possible.

Key to the Hexandrous Species of *Topobea*

1a. Leaves sessile and cordate-clasping; calyx lobes oblong-ovate; petals white, 8–13 mm long; anthers subulate, 5–7 mm long . . . . . *T. cordata*

1b. Leaves distinctly petioled, varying from elliptic-ovate to obovate or subrotund; calyx lobes lance-triangular; petals pink, 4.5–7 mm long; anthers bluntly oblong, 2–2.5 mm long.

2a. Ovary 4-locular, anther pores dorsally inclined at the truncate apex; anther connective elevated dorso-basally into a blunt spurlike appendage . . . . . *T. crassifolia*

2b. Ovary 2-locular, anther pores somewhat ventrally inclined at the truncate apex; anther connective unappendaged dorso-basally (if connective is appendaged then uppermost cauline nodes beset with spreading tufts of hairs).

3a. Leaves thick and leathery when dry, the apex obtuse to rounded, the abaxial surface glandular punctate.

4a. Hemiepiphytic shrub with adventitious roots on the cauline internodes; uppermost cauline nodes beset with caducous tufts of spreading hairs; leaves ovate-elliptic to subrotund; Cerro Jefe, Panama . . . *T. hexandra*

4b. Terrestrial shrub without adventitious roots on the cauline internodes; uppermost cauline nodes lacking tufts of spreading hairs; leaves obovate to oblanceolate; Cerro Tute, Panama . . . . . *T. caliginosa*

3b. Leaves not thick and leathery when dry, the apex caudate-acuminate, the abaxial surface not glandular punctate . . . . . *T. arboricola*

Species Description

1. *Topobea arboricola* Almeda, sp. nov.
Fig. 1

Type. — PANAMA. Bocas del Toro/Chiriquí border: windswept cloud forest on slopes and valleys of the Cerro Colorado region, elev. 1450 m, 27 Jan. 1989, *Almeda et al. 6456* (holotype: CAS!; isotypes: MO!, PMA!).

Frutex epiphyticus. Lamina 3.8–7.1 × 1.6–3.9 cm elliptica vel ovata apice caudato-acuminata vel attenuata basi acuta vel rotundata, 3–5-nervata papyracea et integra, nervis secundariis nervulisque invisis; petioli 0.9–2.8 cm longi. Flores 6-meri sessiles vel subsessiles in quoque nodo superiori singuli; bracteae omnino liberae; bracteae exteriores 2.5–4 × 1.5–4 mm, ellipticae vel ovato-ellipticae apice acuto vel obtuso; bracteae interiores 2–3 × 2–3 mm, ovatae vel suborbiculares apice rotundato. Calycis tubus 0.5 mm longus, lobis 2 mm longis. Petala 5 × 3.5 mm obovata vel obovato-elliptica apice obtuso. Antherae 6, ca. 2 × 0.5 mm oblongae inter se non cohaerentes; connectivum nec prolongatum nec appendiculatum. Ovarium 2-loculare et omnino inferum apice glabro (cono et collo non evoluto).

Epiphytic shrub to 1.5 m tall. Uppermost branchlets glabrous, somewhat compressed and bluntly two-edged; older branches becoming ± rounded with nodular leaf scars. Mature leaves of a pair equal to somewhat unequal in size, glabrous throughout; petioles 0.9–2.8 cm long; mature blades papyraceous, 3.8–7.1 cm long and 1.6–3.9 cm wide, elliptic to ovate, apex caudate-acuminate to attenuate, base acute varying to rounded, margin entire, 3–5-nerved, the outermost intramarginal pair often depressed and inconspicuous, the transverse secondary veins typically not elevated or conspicuous. Flowers erect, solitary in leaf axils of uppermost branches, sessile, subsessile, or with short (1–2 mm) ill-defined peduncles formed by the compressed bases of the outer floral bracts. Floral

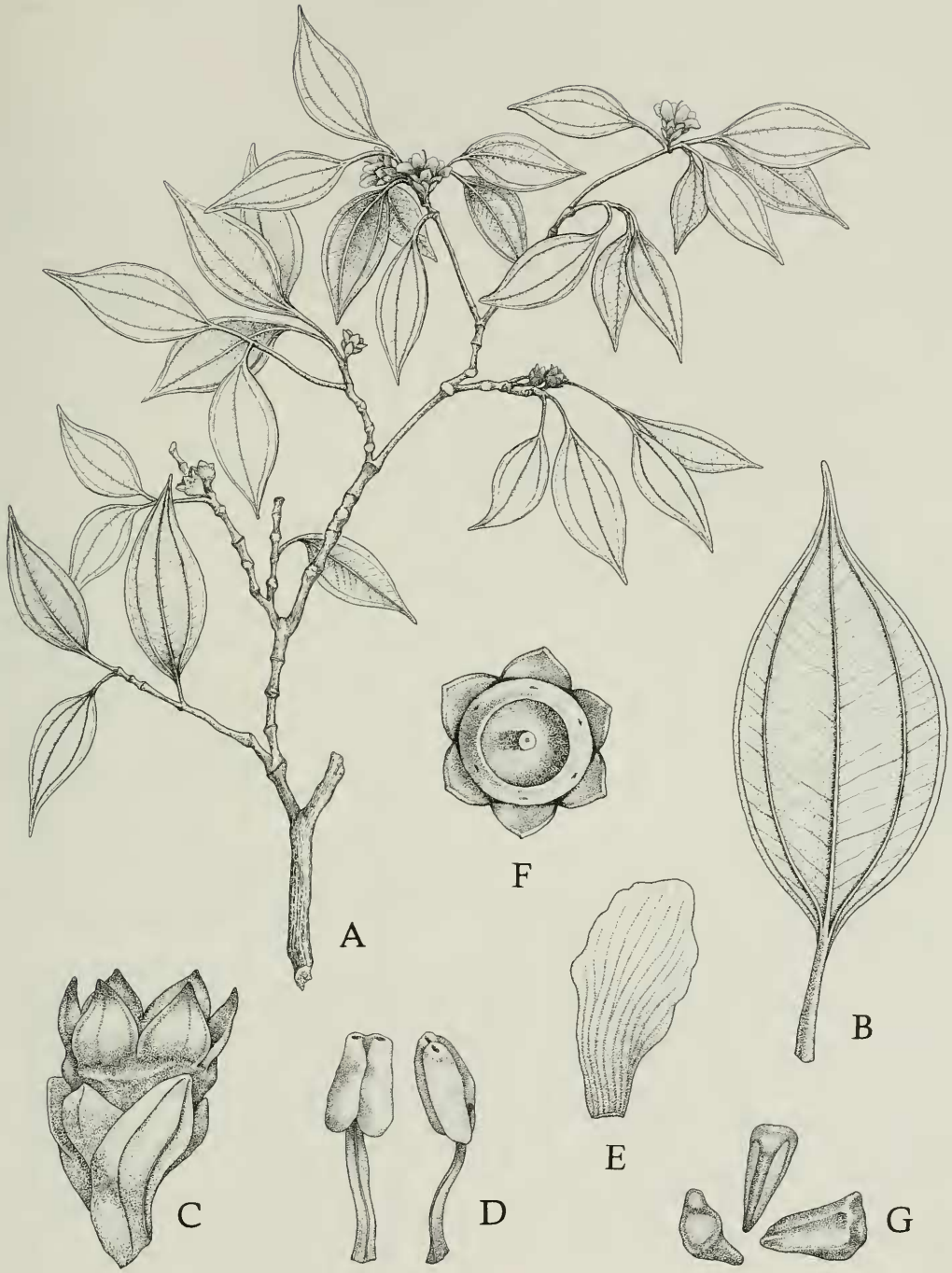

FIGURE 1. *Topobea arboricola* Almeda. A. habit, × ca. ½; B. representative leaf (abaxial surface), × 1; C. young fruiting hypanthium with decussate floral bracts, × 6; D. stamens, ventral view (left) and partial profile view (right), × 7; E. petal (adaxial surface), × 7; F. berry (top view) showing calyx lobes, ovary summit, and torus with staminal filament scars, × 4; G. seeds, × 15. (A, B from the holotype; C-E from *McPherson 12813*, MO; F, G from *McPherson 7739*, CAS.)

bracts free and entire, glabrate or sparingly beset abaxially (mostly toward the apex) with a lanate or stellulate-lepidote, coppery brown indument; outer bracts 2.5–4 × 1.5–4 mm, concave, elliptic to elliptic-ovate, apex acute to obtuse; inner bracts 2–3 × 2–3 mm, depressed-ovate to semicircular, apex rounded. Calyx tube 0.5 mm long; calyx (in fruit) erect, 2 mm long and 2 mm wide basally, deltoid to deltoid-ovate, entire but callose-thickened along the interlobe sinuses, sometimes sparingly beset at the abaxial apex with an indument like that of the floral bracts. Petals 6, sparingly beset with disc-shaped glands when dry, 5 × 3.5 mm, translucent pink, obovate to elliptic-obovate, apex obtuse, entire. Stamens 6, filaments complanate and glabrous, 2.5–3 mm long; anthers 2 mm long, 0.5 mm wide, pale yellow, oblong with two broad pores at the truncate apex; connective barely thickened and unappendaged. Ovary completely inferior, 2-locular, apex glabrous, stylar scar evident but not elevated into a prominent cone or stylar collar. Style somewhat declinate and sigmoid apically, glabrous, 5 mm long; stigma punctiform. Berry 4–6 × 4.5–6 mm, white at maturity. Seeds cuneate to narrowly deltoid, 1 mm long, tan with a smooth, glossy testa.

PHENOLOGY. — Flowering in February, May, July and August; fruiting specimens have been collected in July, December, and January.

DISTRIBUTION. — Known only from wet cloud forests of western Panama from Valle de la Sierpe (Chiriquí) east to Cerro Tute (Veraguas) at 1000–1500 m (Fig. 2).

PARATYPES. — PANAMA. Bocas del Toro/Chiriquí border: above Fortuna dam, along divide trail, ca. 8°45′N, 82°15′W, 4 Dec. 1985, *McPherson 7739* (CAS, MO). Chiriquí: Fortuna dam area, along Quebrada Bonita to E of road, 8°45′N, 82°13′W, 8 Feb. 1984, *Churchill et al. 4759* (MO); Valle de la Sierpe, en dirección SE a lo largo de Quebrada Bonita, 17 May 1987, *Correa et al. 5092* (MO, PMA); Fortuna dam area, N of reservoir, ridge along continental divide and southward from Quebrada de Arena, Aug. 1984 (no day given), *D'Arcy & Todzia 15959* (CAS, MO). Veraguas: trail to Reserva Biológica Serranía de Tute about 0.7 km beyond the Escuela Agricola Río Piedra just outside of Santa Fé, 18 Feb. 1996, *Almeda et al. 7622* (CAS, MO, PMA, US); Distrito de Santa Fé, Serranía de Tute, 8°33′N, 81°07′W, 5 Jul. 1996, *Aranda et al. 2676* (CAS, SCZ); Distrito de Santa Fé, Serranía de Tute, 8°33′N, 81°07′W, 5 Jul. 1996, *Aranda et al. 2657* (CAS, SCZ); vicinity of Cerro Arizona-Tute, above Santa Fé and Altos Piedra, along trail to summit, 8°30′N, 81°10′W, 28 Jul. 1988, *McPherson 12813* (MO).

DISCUSSION. — *Topobea arboricola* appears to be a true epiphytic shrub that never has root contact with the ground. It is distinguished by its 2-locular ovary, comparatively long petioles (0.9–2.8 cm), elliptic to ovate leaves with a caudate-acuminate to long-attenuate apex, and short oblong anthers with unappendaged connectives.

Of the three hexandrous species of *Topobea* with 2-locular ovaries, *T. arboricola* is most similar to *T. caliginosa*. The latter differs in being a terrestrial shrub and in having obovate leaves with an obtuse to rounded apex, shorter petioles (0.5–1 cm), longer floral peduncles (3–5 mm), and abaxial foliar surfaces that are inconspicuously glandular-punctate.

All collections of *T. arboricola* come from a scattering of localities along the Cordillera Central of Panama. For an epiphyte with a dispersed population structure, this species is remarkably uniform in vegetative and reproductive characters. An exception to this homogeneity is exhibited by the Cerro Tute population which has uniformly ovate leaves (vs. elliptic leaves).

ETYMOLOGY. — The epithet for this species, *arboricola*, is derived from the Latin word, arbor, meaning dwelling in a tree, in reference to its epiphytic habit in the forest canopy.

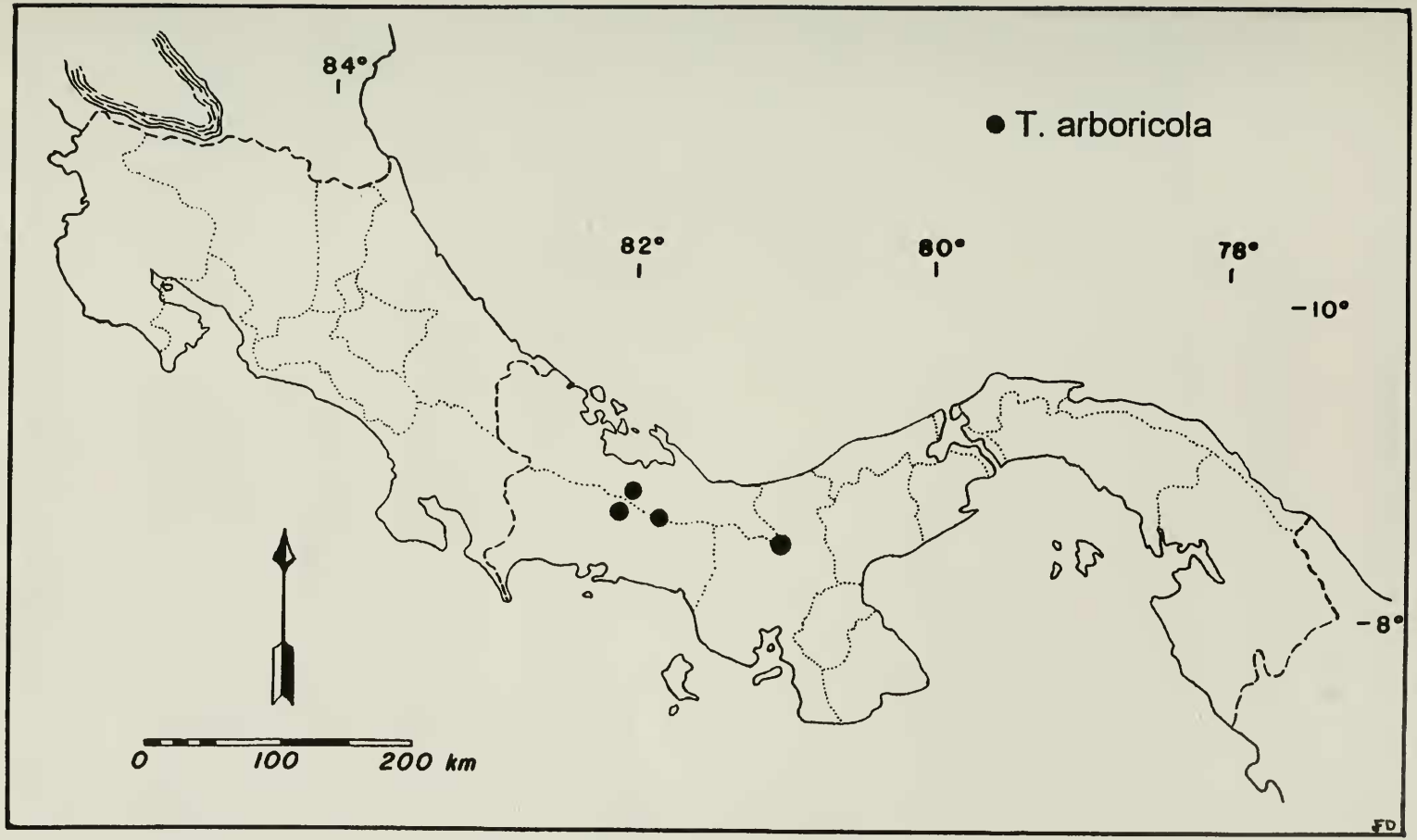

FIGURE 2. Distribution of *Topobea arboricola* in Panama.

2. *Topobea caliginosa* Almeda, Proc. Calif. Acad. Sci. 46(14):317. 1990.

Blakea micrantha Almeda, Rhodora 82:614. 1980.

TYPE. — PANAMA. Veraguas: Cerro Tute ca. 10 km NW of Santa Fé on ridgetop in cloud forest above 1000 m, 19 June 1975, *Mori 6765* (holotype: CAS!; isotype: MO!).

Rigidly branched terrestrial shrub to 1 m tall. Upper cauline internodes quadrangular to distinctly carinate. Young vegetative buds and juvenile foliage commonly beset with a sparse coppery brown furfuraceous indument, otherwise glabrous throughout. Leaves coriaceous and glabrous when dry but inconspicuously punctate abaxially, 1–4 × 0.4–1.6 cm, obovate to oblanceolate, apex obtuse to rounded, base acute to attenuate, the margin entire, often revolute when dry, 3-nerved; petioles 0.5–1 cm long. Flowers solitary in the axils of distal branches, sessile, subsessile or with outermost floral bracts compressed into an ill-defined peduncle 3–5 mm long. Floral bracts rounded at the apex, sparsely floccose to glabrous at maturity, margin entire; outer bracts 3–5 × 2–3 mm, fused at the base for 1–2 mm, elliptic-lanceolate; inner bracts 3–4 × 2–3 mm, free, elliptic-ovate. Calyx lobes bluntly deltoid, 1.5 mm long and 2 mm wide basally. Petals 6, glabrous but sparsely verrucose abaxially when dry, 4.5–6 × 2.5–3 mm, pink, ovate to elliptic-ovate, apex obtuse to rounded, entire. Stamens 6, filaments 2–3.5 × 0.5 mm, erect, glabrous; anthers free, 2 × 0.5–1 mm, linear-oblong and erect, each with two confluent pores at the truncate apex; connective not thickened or appendaged dorsally. Ovary completely inferior, 2-locular, glabrous at the apex which is elevated into a short cone. Style glabrous, 5–6 mm long; stigma punctiform. Berry 4–5 × 3–5 mm. Seeds mostly 1 mm long, cuneate to narrowly pyriform.

PHENOLOGY. — Flowering specimens were collected in February, April, and June; fruiting specimens collected in April, June, and July.

DISTRIBUTION. — Western Panama where it is known only from Cerro Tute (Veraguas) at 1400–1453 m (Fig. 3).

REPRESENTATIVE SPECIMENS EXAMINED. — PANAMA. Veraguas: windswept summit of Cerro Tute, 18 Feb. 1996, *Almeda et al. 7627* (CAS, MO, PMA); distrito de Santa Fé, Serranía de Tute, 8°33′N, 81°07′W, 5 Jul. 1996, *Aranda et al. 2724* (CAS, SCZ); summit of Cerro Tute above Escuela Agricola Alto de Piedra, just W of Santa Fé, 8°32′N, 81°07′W, 5 June 1982, *Knapp & Dressler 5394* (CAS, MO).

DISCUSSION. — This species was originally described as an epiphytic shrub based on information provided by the collector of the type and only known collection at the time (Almeda 1980). During recent field work I have found *T. caliginosa* growing only as a terrestrial shrub above tree line on the shrubby summit of Cerro Tute.

Three other congeners in this hexandrous group of species also occur on Cerro Tute—*T. arboricola*, *T. cordata*, and what may be an undescribed taxon most closely related to *T. hexandra*. The two former taxa appear to be true epiphytic shrubs that grow on trees within the cloud forest zone. The third entity, which grows in the upper zone just below tree line, is a vinelike secondary hemiepiphyte that germinates terrestrially, ascends nearby trees by adventitious roots, and later becomes epiphytic by losing root contact with the ground. This sympatry and parapatry suggest that strong isolating mechanisms are operating to maintain phenotypic distinctions among four closely related species. That this all occurs on a tropical mountain of 1453 m elevation makes it all the more remarkable.

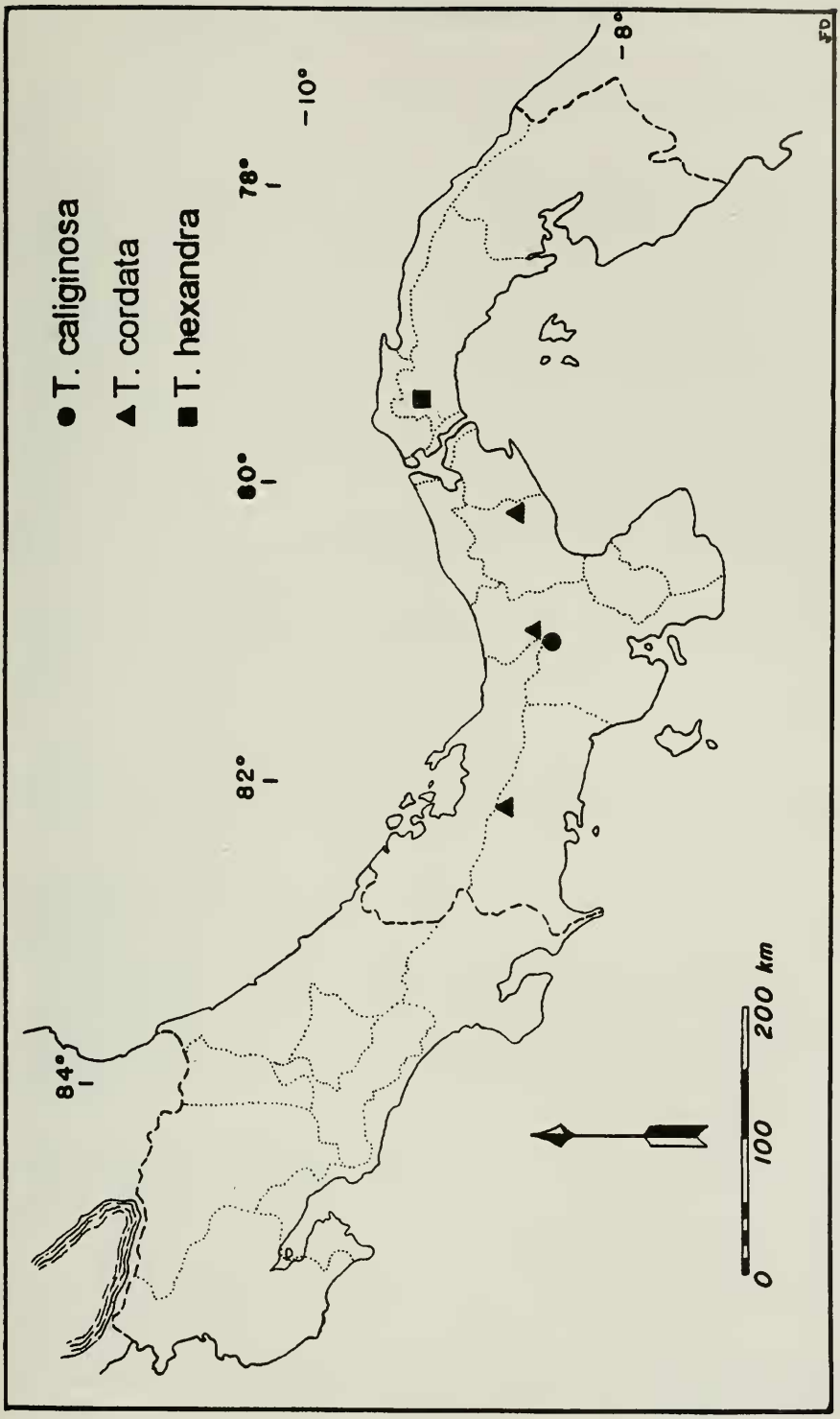

FIGURE 3. Distributions of *Topobea caliginosa*, *T. cordata*, and *T. hexandra* in Panama.

3. *Topobea cordata* Gleason, Phytologia 3:354. 1950.

TYPE. – PANAMA. Coclé: Cerro Pajita, north of El Valle de Antón, elev. 1000–1200 m, *Allen 4178* (holotype: NY!; isotype: MO!)

Epiphytic shrub to 1 m tall. Uppermost internodes ± compressed and quadrisulcate, the angles distinctly carinate sometimes varying to narrowly winged; older branches ± rounded to rounded-quadrate. Leaves of a pair sessile, equal to slightly unequal in size, the younger ones of a pair typically fused basally at the node into a narrow collar, glabrous throughout; mature blades coriaceous, 5.1–12.9 cm long and 3–5.8 cm wide, cordate-clasping to subcordate or ovate, apex acute, base rounded to cordate, margin entire, 5–7-nerved, the secondary veins typically not evident. Flowers erect, coconut-scented (fide *McPherson 8738*), solitary or paired in each upper leaf axil; peduncles 3–4 mm long, conspicuously compressed. Floral bracts entire, glabrate or sparingly beset abaxially (mostly toward the apex) with a coppery brown lanate indument; outer bracts 0.8–1.1 × 0.6–0.9 cm, fused at the base for 2 mm, elliptic, apex acute to obtuse; inner bracts 0.8–0.9 × 0.4–0.6 cm, free to the base, oblong-ovate, apex rounded. Calyx tube 1–1.5 mm long; calyx lobes (at anthesis) 4.5 mm long and 3 mm wide, oblong-ovate, ± entire, essentially glabrous but sometimes beset with a coppery brown lanate indument toward the apex on both surfaces. Petals 6, 0.8–1.3 × 0.4–0.7 cm, translucent-white, obovate, apex rounded, entire. Stamens 6, filaments complanate and glabrous, 6–7 mm long; anthers 5–7 mm long, 1–1.5 mm wide, yellow, subulate with two broad confluent ventrally inclined apical pores; connective not conspicuously thickened and unappendaged. Ovary completely inferior, 4-locular, apex glabrous and elevated into a blunt basally swollen cone 2 mm long. Style somewhat declinate and sigmoid apically, glabrous, 8–9 mm long; stigma truncate. Berry 1 × 1 cm, red at maturity. Seeds narrowly pyriform to cuneate, 1–1.5 mm long, beige, the testa smooth and glossy.

PHENOLOGY. — Flowering from February through May, September and probably during intervening months; the only fruiting specimen was collected in September.

DISTRIBUTION. — Wet cloud forests of western Panama from the Fortuna region (Chiriquí) east to Cerro Pajita (Coclé) at 1050–1250 m (Fig. 3).

REPRESENTATIVE SPECIMENS EXAMINED. — PANAMA. Chiriquí: Fortuna dam region, along Quebrada Arena near continental divide, 8°45′N, 82°15′W, 9 Mar. 1986, *McPherson 8738* (CAS, MO); Fortuna cauce de Quebrada Arena, 9 Apr. 1987, *Valdespino et al. 639* (CAS, PMA). Veraguas: Cerro Tute, trail past agricultural school near Santa Fé, 17 Sep. 1979, *Antonio 1875* (CAS, MO).

DISCUSSION. — The type specimen of this species lacks petals and stamens which accounts for the incomplete descriptions provided in the protologue (Gleason 1950) and subsequent treatment of this species in the Flora of Panama (Gleason 1958). The collection of flowering material with attached stamens facilitated a critical assessment of its generic placement and relationships to other species with six antesepalous stamens (Almeda 1990).

Topobea cordata is characterized by a distinctive suite of characters including sessile cordate-clasping leaves, oblong-ovate calyx lobes, comparatively large (8–13 mm) translucent white petals, and subulate anthers with ventrally inclined apical pores. *Topobea cordata* has a 4-locular ovary like *T. crassifolia*, but the latter has petiolate leaves, lance-triangular calyx lobes, smaller (5–7 mm) pink petals, and short (2–2.5 mm) apically truncate anthers.

One enigmatic collection (*McPherson 9864*, CAS) from the Fortuna region of western Panama resembles *T. cordata* in its overall vegetative morphology and white petals. In calyx shape and staminal details, however, it is a good match for *T. crassifolia*, the species to which *T. cordata* is most closely related. In the size of its floral bracts, hypanthia, and petals this collection also approaches *T. crassifolia*. This kind of character sorting is suggestive of hybridization or introgression between *T. cordata* and *T. crassifolia*. Typical *T. cordata* has also been collected at Fortuna. I have not seen au-

thentic material of *T. crassifolia* from Fortuna but it may well occur there since its range extends both east and west of that region.

4. *Topobea crassifolia* (Almeda) Almeda, Proc. Calif. Acad. Sci. 46(14):318. 1990.

Blakea crassifolia Almeda, Rhodora 82:612. 1980.

TYPE. — PANAMA. Coclé: La Mesa above El Valle in forest on both sides of junction with road to Cerro Pilón, ca. 800 m, 21 Jul. 1974, *Croat 25430* (holotype: CAS!; isotypes: MO!, US!).

Epiphytic shrub to 1 m tall. Uppermost branches quadrangular to rounded, glabrous throughout. Leaves thick, succulent or semisucculent, coriaceous or chartaceous when dry, 1.5–6.5(–12) × 1–4.3 cm, ovate to elliptic-ovate or elliptic-lanceolate, apex acute to attenuate varying to cuspidate or mucronate, base rounded to cordate, the margin entire, 3–5-nerved, often with only the median nerve elevated and conspicuous abaxially, essentially glabrous throughout; petioles 0.1–0.4 cm long. Flowers solitary, paired or in subfasciculate clusters of three to five in axils of distal branches, sessile, subsessile or with ill-defined peduncles 1–2 mm long. Floral bracts glabrous or sometimes beset with an inconspicuous lanate or floccose indument distally, margin entire; outer bracts 5–8 × 2.5–4 mm, fused at the base for about 1 mm, elliptic-lanceolate, apex acute to obtuse or rarely rounded; inner bracts 4–7 × 2.5–4 mm, free but closely subtending the hypanthium, elliptic-ovate, apex acute to rounded or broadly truncate. Calyx lobes lance-triangular, 3–4.5 mm long and 2–2.5 mm wide between sinuses. Petals 6, glabrous and coarsely verrucose, sometimes fringed with a scattering of minute matted hairs, 5–7 × 1.5–2.5 mm, reportedly white or pink, oblong-lanceolate to narrowly oblanceolate, apex acute, base somewhat clawed, entire. Stamens 6, filaments 3.5–4.5 × 0.5 mm, erect, glabrous; anthers free, 2–2.5 × 0.5 mm, linear-oblong and erect distally, each with two confluent dorsally inclined apical pores; connective thickened dorso-basally into a spurlike appendage. Ovary completely inferior, 4-locular and glabrous at the truncate apex. Style glabrous, 6 mm long; stigma punctiform. Berry 6 × 5 mm. Seeds mostly 1 mm long or less, ranging from ovoid or clavate to lunate or pyriform.

PHENOLOGY. — Flowering in February and May through August; fruiting collections have been made in May and August.

DISTRIBUTION. — Cloud forests in central Costa Rica from Braulio Carillo National Park (San José) and vicinity disjunct to Panama from Cerro Colorado (Bocas del Toro) and El Valle de Antón (Coclé) to El Llano-Cartí region (Comarca de San Blas) at 350–1750 m (Fig. 4).

REPRESENTATIVE SPECIMENS EXAMINED. — COSTA RICA. Alajuela/Heredia border: Colonia Virgen del Socorro along road from Costa Rica #9 to the Colonia, 2 Aug. 1976, *J. & K. Utley 5629* (CAS, DUKE, F). San José: Parque Nacional Braulio Carillo. La Montura, 25–30 Jul. 1982, *Todzia et al. 1964* (NY). PANAMA. Bocas del Toro/Chiriquí border: Cerro Colorado, road along top, 13 Aug. 1977, *Folsom et al. 4681* (CAS). Coclé: La Mesa, 4 km N of El Valle de Antón, 6 May 1981, *Sytsma et al. 4364* (CAS, MO); along trail to La Mesa about 4.5 miles beyond El Valle de Antón, 21 May 1970, *Wilbur & Luteyn 11697* (CAS, DUKE, F, MO, US). Comarca de San Blas: El Llano-Cartí road. Nusagandi, 19 km from Interamerican Hwy, 9°19′N, 78°55′W, 26 Aug. 1984, *de Nevers & de León 3767* (CAS, MO); El Llano-Cartí road, km 19.1, 9°19′N, 78°55′W, 1 Jul. 1985, *de Nevers 5943* (CAS, MO); entrada a Nergan Igar, km 15 de la carretera Llano-Cartí, 9°20′N, 78°58′W, 2 Jul. 1994, *Galdames et al. 1243* (CAS, SCZ).

DISCUSSION. — Among the hexandrous species, *T. crassifolia* is the most widely distributed and has the broadest elevational amplitude. Like many woody epiphytes, the fragmented but small population structure of this species has evidently promoted morphological divergence.

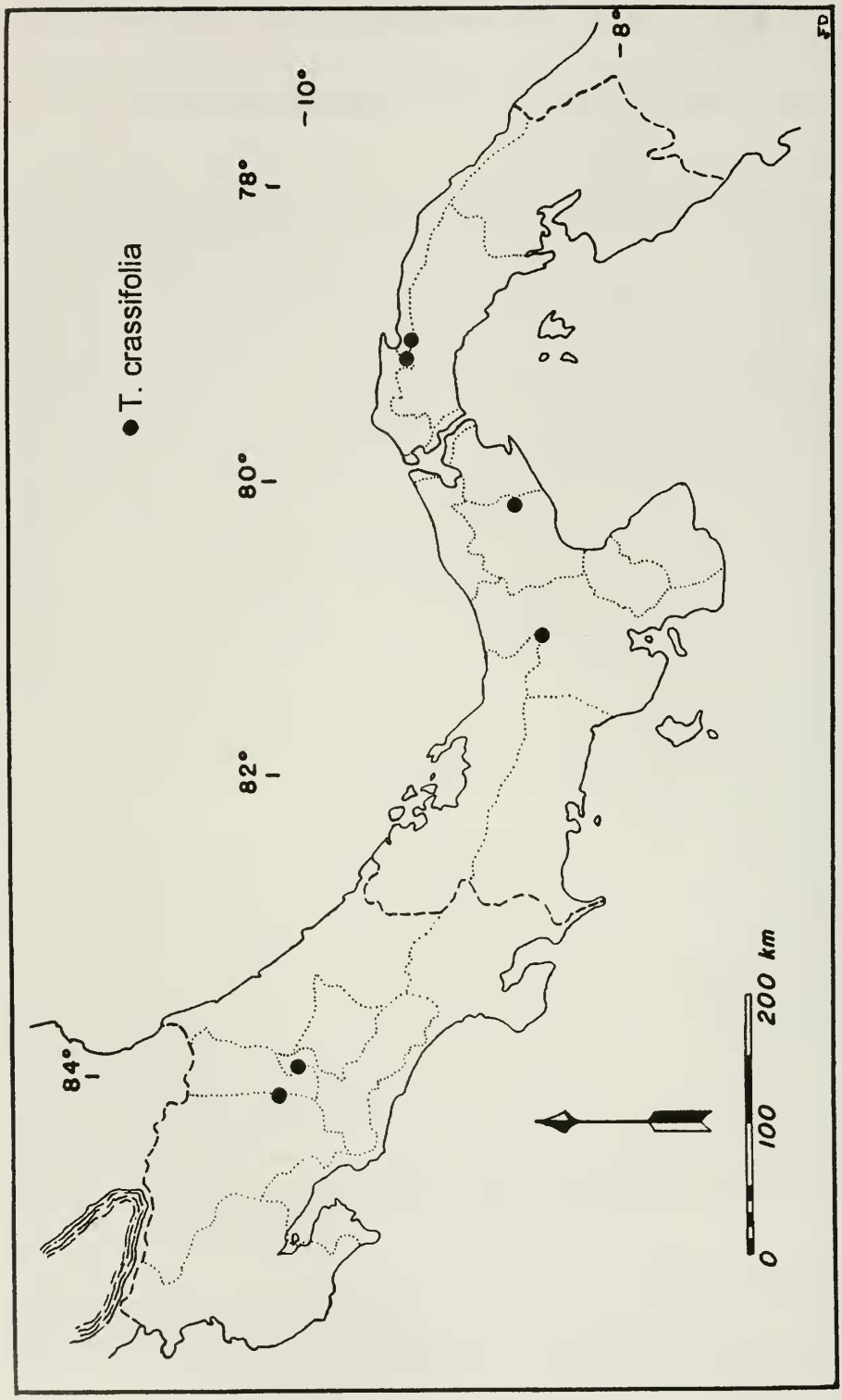

FIGURE 4. Distribution of *Topobea crassifolia* in Costa Rica and Panama.

Most of the known populations of *T. crassifolia* can be distinguished by leaf shape alone. Plants from the type locality near El Valle, Panama, have thick semisucculent leaves that are ovate to elliptic-ovate and bluntly apiculate to obtuse or rounded apically. The Cerro Colorado population in western Panama has smaller (4.5–5 × 1.7–2.5 cm) elliptic to elliptic-ovate leaves that are coriaceous. The northernmost population from central Costa Rica has longer elliptic-ovate to elliptic-lanceolate leaves (5.3–12 cm × 3–3.4 cm) that are thinner, flexuous, and acute to attenuate apically. All of these populations are otherwise identical in other vegetative and reproductive characters. Because of this, I here emphasize their unity and underlying similarities by recognizing a single variable species. Variation of this kind, while striking, is not unprecedented among other epiphytic Melastomataceae. *Leandra subulata* Gleason, for example, is another woody epiphytic melastome with many geographical variants and a comparable montane distribution in Costa Rica and Panama.

Another population from the El Copé region of west-central Panama may also prove to be a geographical variant of *T. crassifolia*. It has ovaries with 4-locules like *T. crassifolia* but its thick leathery leaves are narrowly elliptic, 2.3–3 cm wide, and uniformly long-acuminate basally and apically. This variant is known from two specimens, *Almeda et al. 7650* (CAS) and *Folsom & Robinson 2437* (CAS), both of which are only in bud. These specimens are tentatively excluded from my concept of *T. crassifolia*, pending study of additional material.

5. *Topobea hexandra* Almeda, Proc. Calif. Acad. Sci. 46(14):320. 1990.

TYPE. — PANAMA. Panamá: Cerro Jefe, along summit road and along trail into the Chagres Valley, elev. ca. 900 m, 19 Feb. 1988, *Almeda et al. 5837* (holotype: CAS!; isotypes: CR!, DUKE!, F!, MO!, NY!, PMA!, TEX!, US!).

Hemiepiphytic shrub to 1 m tall adhering to the bark of host trees by nodal and internodal adventitious roots. Upper cauline internodes quadrate to quadrisulcate, glabrous or sparsely covered with spreading, caducous, glandular hairs 1–2 mm long, as are the young petioles and both surfaces of juvenile leaves; older branches rounded, the leaf scars typically swollen. Uppermost nodes beset with brown spreading hairs. Vegetative buds copiously covered with a deciduous brown indument of stellate-lepidote hairs. Leaves coriaceous and glabrous throughout but inconspicuously punctate abaxially, 2–3.9 × 1.1–3 cm, suborbicular to elliptic-ovate, apex rounded varying to obtuse, base obtuse to rounded, margin entire, 3-nerved, often with an additional inconspicuous intramarginal pair; petioles 0.5–1.4 cm long. Flowers erect, solitary or paired in the leaf axils of distal branches, sessile or subsessile with short (to 1 mm) ill-defined peduncles formed by the compressed bases of the outer floral bracts. Floral bracts thick and semisucculent, free and entire, sparingly stellulate-furfuraceous abaxially; outer bracts 5–6.5 × 3–5 mm, concave, ovate to elliptic-ovate, apex obtuse to bluntly mucronate; inner bracts 4–5 × 4–6 mm, broadly ovate to suborbicular, apex rounded. Calyx tube 1 mm long; calyx lobes erect, 2 × 2–2.5 mm, ovate to deltoid-ovate, entire but irregularly roughened along interlobe sinuses, sparingly stellate-lepidote. Petals 6, liberally covered with hyaline disc-shaped glands when dry, 6.5–7 × 4 mm, pink, elliptic-obovate, apex obtuse. Stamens 6, filaments 3 mm long and somewhat declinate; anthers free, 2 × 1 mm, pale yellow turning brownish orange with age, oblong, each with two ventrally inclined pores at the broadly rounded apex, connective slightly thickened and dilated dorso-basally at the filament insertion into a blunt spur up to 0.25 mm long. Ovary completely inferior, 2-locular, glabrous at the apex and not modified into a cone or collar. Style glabrous, 5.5 mm long; stigma punctiform. Berry 5–6 × 4–7.5 mm. Seeds 1–1.5 mm long, beige, bluntly deltoid.

PHENOLOGY. — The only known flowering specimen was collected in February; fruiting specimens have been collected in February, September, October, and December.

DISTRIBUTION. — Known only from low cloud forests at the summit of Cerro Jefe east of the Canal Area in central Panama at 900–1025 m (Fig. 3). The Cerro Jefe region was an important island refugium from the middle Miocene until the land bridge between North America and South America was established ca. 3.5–2.4 million years ago (Graham 1985; Lewis 1971). This geologic history is reflected in the high incidence of vascular plant endemism on Cerro Jefe. Of the approximately 1230 species of plants thought to be endemic to Panama (Carrasquilla 1997), about 150 occur on Cerro Jefe including 6 locally endemic species of Melastomataceae.

REPRESENTATIVE SPECIMENS EXAMINED. — PANAMA. Panamá: summit and S facing slopes of Cerro Jefe, 9 Feb. 1978, *Almeda & Nakai 3459* (CAS); Cerro Jefe along summit road beyond the Intel tower, 3 Feb. 1996, *Almeda et al. 7495* (CAS); Cerro Jefe, along trail on ridge running NE from summit, 18 Dec. 1974, *Mori & Kallunki 3755* (MO); Cerro Jefe, 29 Oct. 1980, *Sytsma 2007* (MO); Cerro Jefe, road leading N from summit, 26 Sep. 1975, *J. T. & F. Witherspoon 8552* (MO).

DISCUSSION. — As noted in the protologue, *T. hexandra* is a common hemiepiphyte in the summit forest of Cerro Jefe, but it appears to be overlooked by most collectors because it has small flowers that are rarely evident to the casual observer without the aid of binoculars (Almeda 1990). This species is variable in indument characters. The uppermost cauline internodes can either be glabrous or sparsely covered with spreading glandular hairs. These glandular hairs are also produced on petioles of juvenile foliage and on upper and lower surfaces of some young leaves, but they commonly fall away with age.

Topobea hexandra is readily distinguished from the other hexandrous species with 2-locular ovaries by its ovate-elliptic to subrotund leaves, dorso-basally appendiculate anther connectives, and dark brown tufts of hairs on the uppermost nodes.

What may be an extreme variant or perhaps an undescribed taxon is known from two collections (*Almeda et al. 7621*, CAS and *Aranda et al. 2733*, CAS) made on Cerro Tute, Panama, in 1996. This entity is also a hemiepiphyte but it has small leaves (0.9–1.4 × 0.4–1 cm) that are obovate with a rounded to emarginate apex. One of these collections is in bud and the other is in young fruit. In view of the small sample size and the lack of mature flowers and fruits, no taxonomic disposition of the Cerro Tute population is possible at this time.

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